

Production and Reproductive output of four Porcelain Crab Species from Northern Chile.

Hernández-Bové¹, P. and Pinheiro, M. A. A.²

¹Museo del Mar, Universidad Arturo Prat, Casilla 121, Iquique, Chile, e-mail: bove@cvmail.cl

²Departamento de Biología Aplicada, FCAV, UNESP Jaboticabal, CRUSTA, Rod. Prof. Paulo Donato Castellane, s/n, 14870-000, Jaboticabal, SP, Brasil, e-mail: pinheiro@fcav.unesp.br

Abstract

Ovigerous females of the porcellanids *Petrolisthes granulosus*, *P. violaceus*, *Allopetrolisthes angulosus* and *A. spinifrons* were collected in a coastal area close to Arica during summer 1999 to compare their fecundity and energetic expenditure for reproduction. Regression analyses were carried out to model the relationship between number of eggs and both carapace length and width. The power function ($y=ax^b$) rendered an adequate fit. The species of the genus *Petrolisthes* produce eggs of higher volume (0.157-0.241 mm³) compared to *Allopetrolisthes* spp. (0.075-0.145 mm³). The inverse pattern was found regarding fecundity (98-104 and 299-711 eggs, respectively). In spite of such differences, the reproductive output was very similar among the analysed species, except for *P. violaceus* in which the obtained value was very reduced.

Key words: *Petrolisthes*, *Allopetrolisthes*, production, fecundity, reproductive output

Introduction

Porcelain crabs constitute one of the most characteristic families in the intertidal habitats of the American Pacific (Viviani, 1969). The presence of the Porcellanidae in this region has been described by many researchers, who reported valuable information on the biogeography (Haig, 1960; Garth *et al.*, 1967; Carvacho, 1980; Boschi, 2000) and ecology (Viviani, 1969; Brattström, 1990) of some representatives of this family. Yet, some aspects of their biology, including reproduction, are still largely unknown. Some researchers had focused on the larval development (Saelzer *et al.*, 1986; Albornoz and Wehrtmann, 1996; Wehrtmann *et al.*, 1996), latitudinal variation of some reproductive characteristics (Hernández-Bové, *in press*), production and energy allocation for reproduction (Antezana *et al.*, 1965; Sanhueza *et al.*, 1975; Lardies and Wehrtmann, 1996), and latitudinal variation of the reproductive process (Hernández-Bové, *in press*).

In Chile, the family Porcellanidae is represented by 16 species distributed in five genera (Carvacho, 1980), most of them free living species, while some are found associated with sessile organisms, e.g. tube-dwelling polychaetes, anemones and a number of echinoderms (Haig, 1960; Viviani, 1969). In the Chilean coast, those species are commonly distributed in delimited belts within the intertidal zone (Antezana *et al.*, 1965). This peculiar species distribution is an outcome of physiological mechanisms developed through processes of environmental adaptation. As a result, interesting reproduction strategies emerged, namely contrasting patterns of egg production (number and volume of eggs) and energy allocation to the reproductive process.

In this study, the fecundity and egg volume are quantified and compared among four intertidal porcelain crab species, and the energy allocation for reproduction is estimated. The results presented may provide a basis for further research in this area and contribute to a better understanding of the auto-ecology of marine species in northern Chile.

Material and Methods

Ovigerous females of the porcelain crab species *Petrolisthes granulatus* (Guerín, 1835), *Petrolisthes violaceus* (Guerín, 1831), *Allopetrolisthes angulosus* (Guerín, 1835) and *Allopetrolisthes spinifrons* (H. Milne-Edwards, 1837) were collected during the summer of 1999 from the rocky coast at Sector Corazones to southern Arica (Fig. 1). The sampling season was reduced as possible to avoid temporal changes of the reproductive parameters of the studied populations (Díaz, 1980; Jones, 1980). At each sampling site, a large number of individuals were collected manually over their entire intertidal range during spring tides. All ovigerous females were separated in individual plastic bags, due to limb loss and egg detachment, and transported to the Department of Chemistry at the Arturo Prat University, where they were frozen (-15°C) and stored until later analyses.

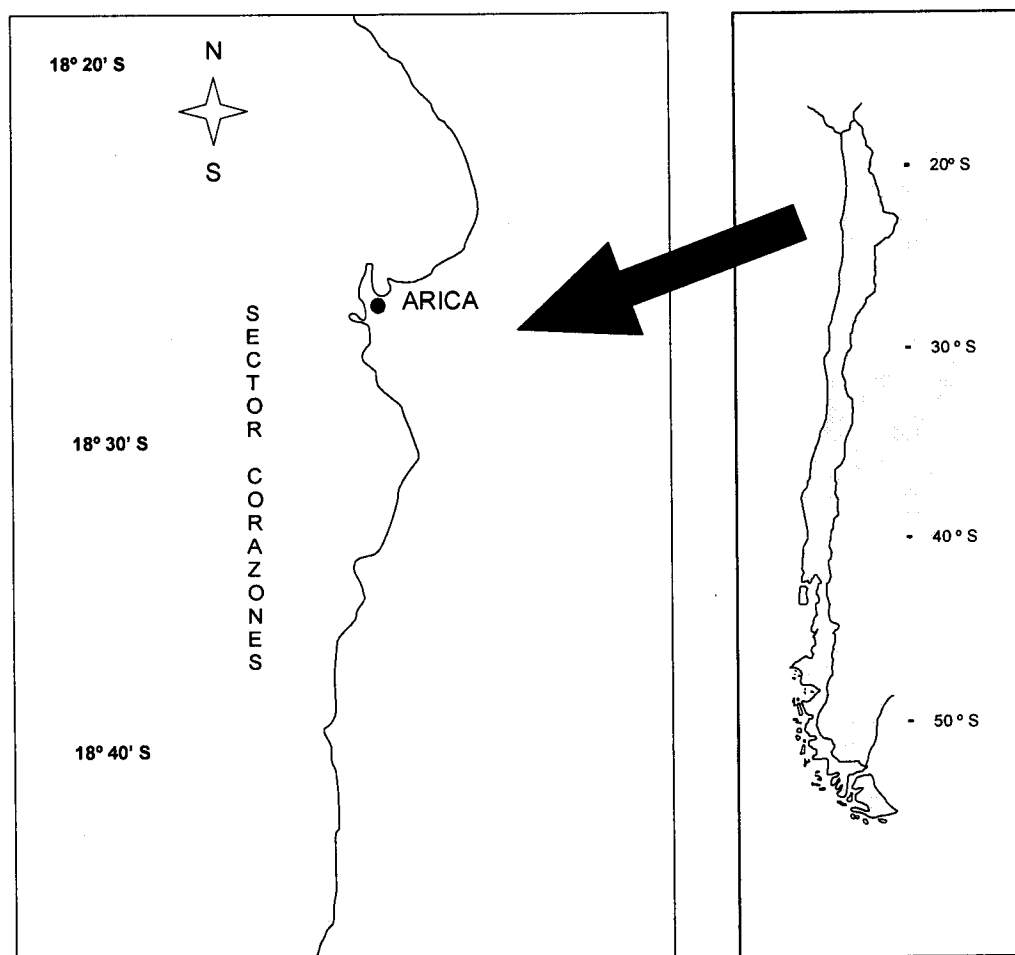


Figure 1: Indication of "Sector Corazones" at the northernmost coast of Chile, the study area where ovigerous females of the species *Petrolisthes granulatus*, *P. violaceus*, *Allopetrolisthes angulosus* and *A. spinifrons* were collected.

Nauplius

All specimens were identified following the identification key for anomuran crustaceans proposed by Guzmán (1999) and measured at their carapace length (CL), from the rostrum tip to the posterior margin, and carapace width (CW), as the distance between lateral carapace margins. All measurements

were recorded with the aid of a stereomicroscope provided with a *camera lucida* to the nearest 0.1 mm. The maturity size was established as the 50th percentile of the overall size frequency distribution for the ovigerous females, as determined after fitting a sigmoid curve to the relationship between the percentage of ovigerous females and size, using 0.1mm size classes (Wenner *et al.*, 1974).

After removing the egg mass of each ovigerous female, number of eggs (N) was determined by direct counting under a Leitz stereomicroscope. The development degree of incubated embryos (DE) was classified in three stages according to Wehrtmann (1990). Stage I: egg recently extruded, yolk uniform without eyespots. Stage II: Eyespots hardly visible. Stage III: Eyes clearly visible and fully developed, abdomen free.

For each species, scatter plots were obtained for the relationships N *vs.* CL and N *vs.* CW. These relationships were then subjected to regression analysis in order to determine the most adequate equation to represent fecundity variability according to size. The fitting adequacy of each tested function was judged by comparing the determination coefficients (R^2) obtained.

In order to estimate egg volume (EV), 20 eggs of each ovigerous female were separated and measured under a Nikon microscope supplied with a micrometric ocular. Eggs were considered spherical and their volume was calculated according to the formula, $EV=1/6((b^2a)\pi)$ (see Corey and Reid, 1991). The volume increment during the incubation period was calculated using the equation proposed by Kobayashi and Matsuura (1995). The energetic allocation during the reproductive process was estimated by measuring the reproductive output (RO) of recently extruded eggs. For that, females and their corresponding egg masses were dried at 60°C for 24 h, and the resulting values used in the formula $RO = DW_{EM}/DW_{WE}$ (DW_{EM} = dry weight of the egg mass; DW_{WE} = dry weight of female without eggs), proposed by Clarke *et al.* (1991). Finally, the average values of each reproductive variable were compared in an ANOVA, and post-hoc Tukey tests (Zar, 1999) were run ($p<0.05$) to verify if interspecific and intergeneric differences are significant.

Results

During the study period a total of 179 ovigerous females were examined, comprising four species and two genera (*Petrolisthes* and *Allopetrolisthes*). It was observed that average size of *Petrolisthes violaceus* (11.3 ± 17.1 mm) and *Allopetrolisthes spinifrons* (13.1 ± 1.99 mm) is significantly higher than their respective congeners ($p<0.001$) (Table I). Assuming that the minimum size of ovigerous females is a reliable approximation to the actual size at the onset of sexual maturity (Giese, 1959; Jones, 1980), it can be considered that *P. granulosus* and *A. angulosus* develop into mature individuals (5.1 and 6.5 mm CW, respectively) earlier than *P. violaceus* and *A. spinifrons* (7.4 and 10.8 mm CW, respectively). Average fecundity varied from 98 ± 44 eggs, as observed in *P. granulosus*, to 711 ± 465 eggs, as found in *A. spinifrons*. Post-hoc tests indicate that fecundity in *P. granulosus* and *P. violaceus* are not significantly different ($p>0.05$). Otherwise, the difference of average production between the *Allopetrolisthes* species is significant (see Table I).

By comparing their maturity size, it may be concluded that *P. granulosus* and *A. angulosus* undergo a precocious maturity compared to the other examined species (Table II).

In all cases, the number of eggs produced (N) is strongly correlated with carapace width and length (see Table III), and the power function ($y=ax^b$) was found to be adequate to fit this relationship (Fig. 2). The increase of egg size during embryogenesis vary considerably between these two genera. Egg volume in the *Petrolisthes* species ($0.157-0.241$ mm³) is higher than in *Allopetrolisthes* ($0.075-0.145$ mm³), but the average increase in the former species is lower, i.e. 31.6 and 49.5%, respectively (see Table IV), according to the equation proposed by Kobayashi and Matsuura (1995). Average fecundity in

Petrolisthes is however lower than in *Allopetrolisthes* (98-104 and 299-711 eggs, respectively). Overall and within-stage comparisons rendered no statistical differences for egg volume between the *Allopetrolisthes* species (Table I, Table IV, $p > 0.05$).

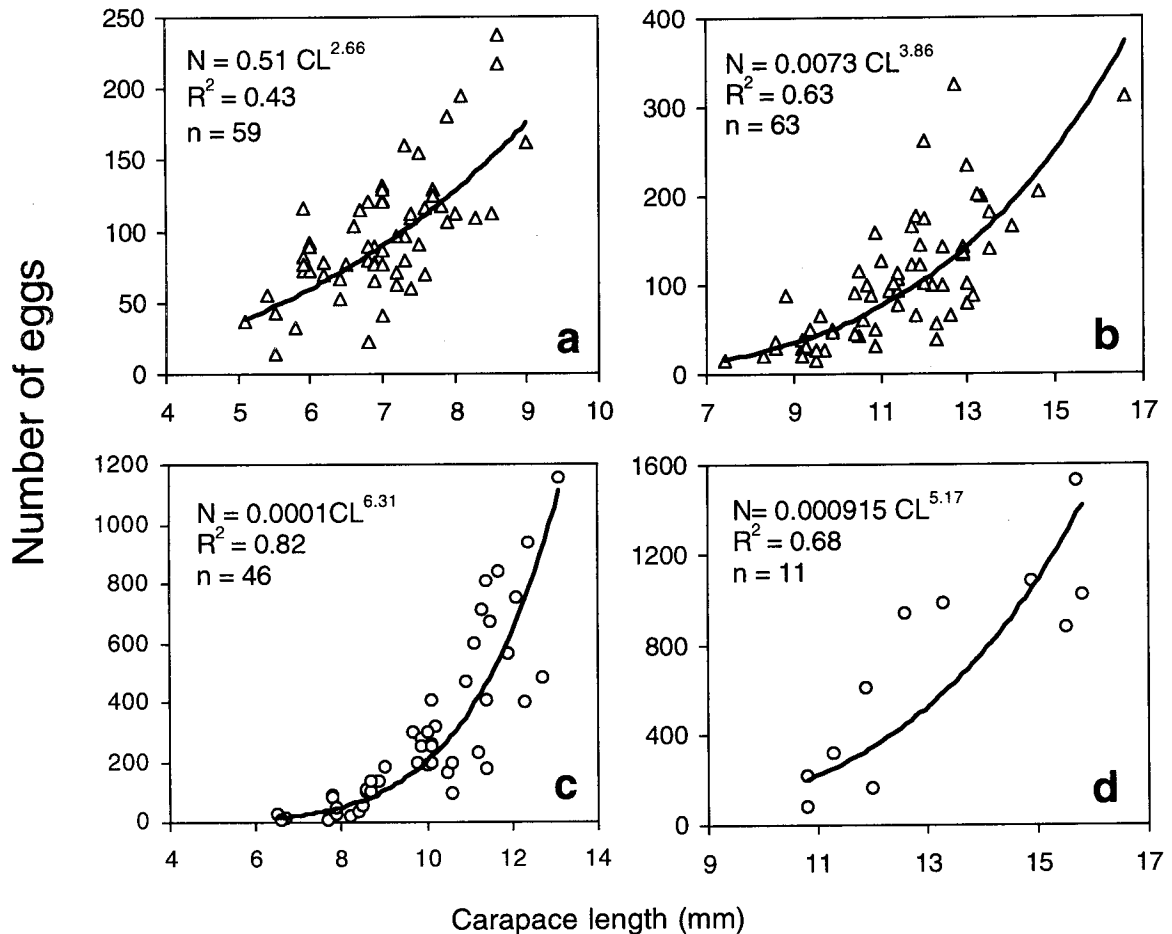


Figure 2: Fitted linear and power functions for the relationship between number of eggs (N) and carapace length (CL) for *Petrolisthes granulosus* (a), *Petrolisthes violaceus* (b), *Allopetrolisthes angulosus* (c) and *Allopetrolisthes spinifrons* (d).

Energy allocation for reproduction varied from 2.0 to 5.5% for *Petrolisthes* and 2.4 to 4.7% for *Allopetrolisthes*. The species showing the lowest and highest values of energy allocation for reproduction are *P. violaceus* and *P. granulosus*, respectively (Table V). Except for *P. violaceus*, average reproductive output does not differ significantly among species ($p > 0.05$).

Discussion

Compared to other crustaceans, porcelain crabs are small organisms presenting relatively low fecundity (Reid and Corey, 1991). In Chile, Antezana *et al.* (1965) described the biology of 10 species, thus providing initial information concerning production and size of females along the coast of Valparaiso.

The size at maturity based on the smallest size of ovigerous females and on the 50th percentile of their cumulative frequency distribution provided very similar results in this study. The size of the smallest ovigerous females were also used by Giese (1959) and Jones (1980), and may be considered as valid to represent size at maturity in a given species.

Values of carapace width and number of eggs produced by females at Arica are similar to those previously reported by other authors (see Table VI). Unfortunately, the lack of average values prevents

Table I: Range and average values for carapace length, number of eggs produced and egg volume for females of four species of intertidal porcellanids from northern Chile (SD = standard deviation; n = sample size).

Species	n	Carapace Length (mm)			Number of eggs (N)			Egg Volume (mm ³)		
		Range	Average	SD	Range	Average	SD	Range	Average	SD
<i>P. granulosus</i>	59	5.1-9.0	7.0 a	0.9	14-237	98 a	44	0.129-0.243	0.184 a	0.02
<i>P. violaceus</i>	63	7.4-16.6	11.3 c	1.7	16-325	104 a	70	0.119-0.329	0.210 b	0.03
<i>A. angulosus</i>	46	6.5-13.1	9.9 b	1.7	8-1153	299 b	280	0.057-0.128	0.089 c	0.02
<i>A. spinifrons</i>	11	10.8-15.8	13.1 d	2.0	83-1527	711 c	465	0.090-0.173	0.119 c	0.03
F			109.84			42.96			149.98	
P			<0.001			<0.001			<0.001	

Average values sharing the same letter are not significantly different (p>0.05).

Table II: Size frequency and cumulative size frequency distributions of ovigerous females in four intertidal porcellanid species from northern Chile (CL = carapace length; fi = absolute frequency of the *i*th class; Fi = percentile of the cumulative distribution at the *i*th class).

Size Classes CL (mm)	<i>P. granulosus</i>		<i>P. violaceus</i>		<i>A. angulosus</i>		<i>A. spinifrons</i>	
	fi	Fi	fi	Fi	fi	Fi	fi	Fi
5 - 6	12	20.3	-	-	-	-	-	-
6 - 7	22	57.6	-	-	3	6.5	-	-
7 - 8	19	89.8	1	1.6	5	17.4	-	-
8 - 9	6	100.0	4	7.9	9	37.0	-	-
9 - 10	-	-	11	25.4	6	50.0	-	-
10 - 11	-	-	11	42.9	9	69.6	2	18.2
11 - 12	-	-	15	66.7	9	89.1	3	45.5
12 - 13	-	-	13	87.3	4	97.8	1	54.6
13 - 14	-	-	6	96.8	1	100.0	1	63.6
14 - 15	-	-	1	98.4	-	-	1	72.7
15 - 16	-	-	-	-	-	-	3	100.0
16 - 17	-	-	1	100.0	-	-	-	-
Maturity size (mm) at 50%	7.0		11.4		10.0		12.3	

more precise interspecific comparisons to be done. At Arica, females of the genus *Petrolisthes* produce a lower number of eggs compared to *Allopetrolisthes* (14-325 and 8-1,527 eggs, respectively). Considering the average size of *P. granulosus* (7.0 ± 0.9 mm CW), *A. angulosus* (9.9 ± 1.7 mm CW) and *A. spinifrons* (13.1 ± 2.0 mm CW), variations of carapace width might explain at some extent the interspecific differences of fecundity.

According to Corey and Reid (1991), there is a strong relationship between egg production and size. Reid and Corey (1991) state that number of eggs produced is primarily a function of egg shape and the area they occupy. The results presented herein do not follow Corey and Reid's (1991) trend, since the larger *P. violaceus* (11.3 ± 1.7 mm CW) presents a lower egg production (104 ± 70 eggs) compared to *A. angulosus*.

Egg volume should be considered in intraspecific comparisons of fecundity, because its increase through brooding may cause a decrease of fecundity (Thorson, 1950; Clarke, 1979; 1982; Clarke *et al.*, 1991; Gorny *et al.*, 1992).

The size-specific fecundity relationships of porcellanid are adequately fit by the linear function $y = a + bx$ (Antezana *et al.*, 1965; Sanhueza *et al.*, 1975; Reid and Corey, 1991). Mathematical models used to adjust such relationships are not usually grounded in any theoretical assumptions of biological processes. In fecundity analyses, the relationship between the egg mass, a three dimensional variable, and female size, a unidimensional parameter, can be more effectively represented by power functions such as $y = ax^b$ and $y = a + bx^3$. According to Pinheiro and Terceiro (2000), the function chosen to model this relationship have to explain an array of biological variability, for what the power function may be particularly appropriate.

Compared to other members within the Porcellanidae, *Petrolisthes* females produce relatively large eggs while those produced by *Allopetrolisthes* are among the smallest in the family (see Table VII). *A. angulosus* and *A. spinifrons* produce smaller eggs, considering both size and volume, than *Petrolisthes* species. Taking into account the size variation, this provides further support for the importance of egg volume since space availability for egg production decreases with increasing egg volume.

Table III: Regression equations for fecundity in four porcellanids comprising the genus *Petrolisthes* and *Allopetrolisthes* (CL = carapace length; CW = carapace width; N = number of eggs; n = sample size; R² = determination coefficient).

Species	x	n	Function	R ²	F
<i>Petrolisthes granulosus</i>	CL	59	$N = 0.51 CL^{2.66}$	0.43	43.8 *
	CW	59	$N = 0.72 CW^{2.59}$	0.39	36.5 *
<i>P. violaceus</i>	CL	63	$N = 0.0073 CL^{3.86}$	0.63	73.9 *
	CW	63	$N = 0.0079 CW^{3.97}$	0.66	78.2 *
<i>Allopetrolisthes angulosus</i>	CL	46	$N = 0.0001 CL^{6.31}$	0.82	88.9 *
	CW	46	$N = 0.00001 CW^{5.94}$	0.82	104.5 *
<i>A. spinifrons</i>	CL	11	$N = 0.000915 CL^{5.17}$	0.68	19.1 *
	CW	11	$N = 0.00118 CW^{5.46}$	0.74	25.9 *

* $p < 0.001$

Nauplius Lardies and Wehrtmann (1996) report that embryonic growth for *Petrolisthes laevigatus* along the coast of central – southern Chile is constrained by the thickness and resistance of the egg membrane. In the other hand, size increase of eggs during incubation is often related to the duration of embryonic development (Steele and Steele, 1975; Clarke, 1982). Species subjected to a high desiccation pressure, as *P. granulosus* and *P. violaceus*, are thus expected to produce thick egg membranes as to avoid water loss. This would also constrain embryonic growth, a fact that could explain the results from intergeneric

comparisons regarding increase of egg volume (see Table IV). It should be noted, however, that additional information is needed to support such a pattern.

Table IV: Egg volume (EV) variation through the incubation period in four porcellanids from northernmost Chile (n = sample size; I-III = percentage of volume increment during embryonic development; EV = volume of eggs in mm^3).

Species	Development stage						I-III (%)
	S-I		S-II		S-III		
	n	EV	n	EV	n	EV	
<i>P. granulatus</i>	18	0.157 b	20	0.179 b	21	0.213 b	35.7
<i>P. violaceus</i>	32	0.189 c	17	0.222 c	14	0.241 c	27.5
<i>A. angulosus</i>	24	0.075 a	15	0.103 a	7	0.111 a	48.0
<i>A. spinifrons</i>	4	0.096 a	4	0.123 a	3	0.145 a	51.0

Average values sharing the same letter are not significantly different ($p > 0.05$).

Table V: Reproductive output of ovigerous females of different porcellanid species from the coast of Chile. Data from individuals bearing early embryos (SD = standard deviation).

Species	Author	Reproductive Output (%)		
		Latitude	Mean	SD
<i>P. granulatus</i>	This study	18°33'S	5.5 b	3.0
	Hernández-Bové (<i>in press</i>)	18°33'S	3.7	2.3
	Hernández-Bové (<i>in press</i>)	25°20'S	6.5	3.0
<i>P. violaceus</i>	This study	18°33'S	2.0 a	1.1
<i>P. laevigatus</i>	Lardies and Wehrtmann (1996)	39°49'S	5.7	3.3
<i>A. angulosus</i>	This study	18°33'S	4.7 b	3.6
<i>A. spinifrons</i>	This study	18°33'S	2.4 b	2.2

Average values sharing the same letter are not significantly different ($p > 0.05$).

Table VI: Published information on the fecundity and body size for porcellanid species present in the coast of Chile (CL = carapace length; N = number of eggs).

Species	Author	CL (mm) Range	N Range
<i>Allopetrolisthes punctatus</i>	Antezana <i>et al.</i> (1965)	21.9-39.4	540-16,380
<i>A. spinifrons</i>	Antezana <i>et al.</i> (1965)	6.6-16.4	121-4,548
<i>A. angulosus</i>	Antezana <i>et al.</i> (1965)	5.0-14.0	18-2,580
<i>Pachycheles grossimanus</i>	Antezana <i>et al.</i> (1965)	20.5	5,968
<i>Liopetrolisthes mitra</i>	Antezana <i>et al.</i> (1965)	5.0-9.9	62-543
<i>Petrolisthes violaceus</i>	Haig (1960)	6.7-18.2	Not available
<i>P. tuberculatus</i>	Antezana <i>et al.</i> (1965)	6.4-18.4	85-3,683
<i>P. laevigatus</i>	Lardies and Wehrtmann (1996)	8.5-18.2	56-1,141
<i>P. granulatus</i>	Hernández-Bové (<i>in press</i>)	4.3-10.5	15-380

Table VII: Average egg volume during early development stages for 11 porcellanid species (EV = volume of eggs in mm³).

Species	Author	Locality	EV (mm ³)
<i>Megalobrachium soriatum</i>	Reid and Corey (1991)	Atlantic, Florida	0.067
<i>Pachycheles ackleianus</i>	Reid and Corey (1991)	Gulf of México, Florida	0.124
<i>P. monilifer</i>	Reid and Corey (1991)	Atlantic, Florida	0.200
<i>P. rugimanus</i>	Reid and Corey (1991)	Gulf of México, Florida	0.248
<i>Petrolisthes armatus</i>	Reid and Corey (1991)	Pacific, Panamá	0.050
<i>P. zacaе</i>	Reid and Corey (1991)	Indian River, Florida	0.124
<i>P. haigae</i>	Reid and Corey (1991)	Pacific, Panamá	0.121
<i>P. granulosis</i>	Hernández-Bové (<i>in press</i>)	Arica, Chile	0.164
<i>P. laevigatus</i>	Lardies and Wehrtmann (1996)	Valdivia, Chile	0.226
<i>Polyonyx gibbesi</i>	Reid and Corey (1991)	Indian River, Florida	0.088
<i>Porcellana sayana</i>	Reid and Corey (1991)	Atlantic, Florida	0.110

Petrolisthes granulosis and *P. violaceus* present a reproductive output (RO) similar to the values obtained for *P. laevigatus* and *P. granulosis* (5.6% and 3.7%, respectively) at two sites in the northern and central-southern Chile. Energy allocated for reproduction in *P. violaceus* and *A. spinifrons* is out of the range found by Hines (1992) for brachyurans (from 3% to 22% of total body weight), and much lower than the values obtained by caridean shrimps from temperate and polar regions which vary from 11.8 and 24.2% in *Notocrangon antarcticus* and *Pandalus montagui*, respectively (see Clarke, 1987 and Clarke *et al.*, 1991). The data from pandalid and hippolytid shrimps suggest that the reproductive output of polar species is much lower than in temperate species (Clarke, 1987). A geographical trend of this variable might be thus presumed to take place. Hernández-Bové (*in press*) reports that reproductive output in *P. granulosis* varies according to the inverse latitudinal trend, which raises interesting questions for future research.

References

- Albornoz, L. and Wehrtmann, I. 1996. Aspects of the reproductive biology of *Petrolisthes laevigatus* (Guerín, 1835) (Decapoda: Anomura: Porcellanidae). Part. II: description on the larval development, including the first crab stage, cultivated under laboratory conditions. *Archive of Fishery and Marine Research*, 43: 137-157.
- Antezana, T.; Fagetti, E. and López, M. T. 1965. Observaciones bioecológicas en decápodos comunes de Valparaíso. *Revista de Biología Marina, Valparaíso*, 12: 1-60.
- Boschi, E. E. 2000. Species of decapod crustaceans and their distribution in the american marine zoogeographic provinces. *Revista de Investigación y Desarrollo Pesquero*, 13: 1-136.
- Brattström, H. 1990. Intertidal ecology of the northernmost part of the Chilean Archipelago. *Sarsia*, 75: 107-160.
- Carvacho, A. 1980. Los porcelánidos del Pacífico Americano: Un Análisis biogeográfico (Crustacea: Decapoda). *Anuario Centro de Ciencias Marinas y Limnológicas. Universidad Autónoma México*, 7 (2): 249-258.

- Clarke, A. 1979. On living in cold water: K-strategies in Antarctic benthos. *Marine Biology*, 55: 111-119.
- Clarke, A. 1982. Temperature and embryonic development in polar marines invertebrates. *International Journal of Invertebrates and Reproduction*, 5: 71-82.
- Clarke, A. 1987. Temperature, latitude and reproductive effort. *Marine Ecology Progress Series*, 38: 89-99.
- Clarke, A.; Hopkins, C. C. E. and Nilssen, E. M. 1991. Egg size and reproductive output in the deepwater prawn *Pandalus borealis* Kroyer, 1838. *Functional Ecology*, 5: 724-730.
- Corey, S. and Reid, D. M. 1991. Comparative fecundity of decapod crustaceans, I. The fecundity of thirty-three species of nine families of caridean shrimp. *Crustaceana*, 60 (3): 270-294.
- Diaz, H. 1980. The mole crab *Emerita talpoida* (Say): a case of changing life history pattern. *Ecological Monographs*, 50: 437-456.
- Garth, J.; Haig, J. and Yaldwin, J. C. 1967. The Decapod Crustacea of the Royal Society Expedition to Southern Chile, 1958-59. *Transactions of the Royal Society New Zealand*, 8 (16): 169-187.
- Giese, A. C. 1959. Comparative physiology: annual reproductive cycles of marine invertebrates. *Annual Review Physiology*, 21: 547-576.
- Gorny, M.; Arntz, W. E.; Clarke, A. and Gore, D. J. 1992. Reproductive biology of caridean decapods from the Weddell Sea. *Polar Biology*, 12: 111-120.
- Guzmán, G. 1999. Clave para los Crustáceos Decápodos Anomuros Marinos de Chile. Ediciones Campus. Universidad Arturo Prat, Iquique, Chile. 53 pp.
- Haig, J. 1960. The Porcellanidae (Crustacea: Anomura) of the Eastern Pacific. Allan Hancock Pacific expedition. 24: 1-440.
- Hernández-Bové, P. *In press*. Clino reproductivo latitudinal en *Petrolisthes granulosus* (Decapoda: Anomura: Porcellanidae) del norte de Chile. *Investigaciones Marinas, Valparaíso*.
- Hines, A. 1992. Allometric constraints and variables of reproductive effort in brachyuran crabs. *Marine Biology*, 69: 309-320
- Jones, M. B. 1980. Reproductive ecology of the estuarine burrowing mud crab *Helice crassa* (Grapsidae). *Estuarine, Coastal and Marine Science*, 11: 433-443.
- Kobayashi, S. and Matsuura, S. 1995. Egg development and variation of egg size in the Japanese Mitten Crab *Eriocheir japonicus* (de Haan). *Benthos Research* 48: 29-39.
- Lardies, M. A. and Wehrtmann, I. S. 1996. Aspects of the reproductive biology of *Petrolisthes laevigatus* (Guerín, 1835) (Decapoda: Anomura: Porcellanidae). Part I: Reproductive output and chemical composition of eggs during embryonic development. *Archive of Fishery and Marine Research*, 43(2): 121-135.
- Pinheiro, M. A. A. and Fransozo, A. 1995. Fecundidade de *Pachycheles haigae* Rodrigues da Costa, 1960 (Crustacea, Anomura, Porcellanidae) em Ubatuba (SP), Brasil. *Revista Brasileira de Zoologia*, 55(4): 623-631.
- Pinheiro, M. A. A. and Terceiro, O. S. L. 2000. Fecundity and reproductive output of the speckled swimming crab *Arenaeus cribrarius* (Lamarck, 1818) (Brachyura, Portunidae). *Crustaceana*, 73(9): 1121-1137.
- Reid, D. M. and Corey, S. 1991. Comparative fecundity of decapod crustaceans, II. The fecundity of fifteen species of anomuran and brachyuran crabs. *Crustaceana*, 61(2): 175-189.
- Saelzer, H.; Quintana, R. and Quiñones, R. 1986. Larval development of *Petrolisthes granulosus* (Guerín, 1835) (Decapoda: Anomura: Porcellanidae) under laboratory conditions. *Journal of Crustacean Biology*, 6: 804-819.
- Sanhueza, E.; Bahamonde, N. and Lopez, M. T. 1975. *Petrolisthes granulosus* (Guerín, 1835) en biocenosis supramareales de El Tabo (Crustacea: Decapoda: Anomura). *Boletín Museo Nacional de Historia Natural*, 34: 121-136.
- Steele, D. H. and Steele, V.J. 1975. Egg size and duration embryonic development in Crustacea. *International Review Hydrobiology*, 60(5): 711-715.
- Thorson, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biological Reviews*, 25: 1-45.

- Viviani, C. 1969. Los Porcellanidae (Crustacea: Anomura) Chilenos. Studies on Neotropical Fauna and Environment, 6: 40-56.
- Wehrtmann, I. S. 1990. Distribution and reproduction of *Ambidexter panamense* and *Palaemonetes schmittii* in Pacific Costa Rica (Crustacea: Decapoda). Revista Biología Tropical, 38(2A): 327-329.
- Wehrtmann, I. S.; Albornoz, L.; Veliz, D. and Pardo, M. 1996. Early development stages, including the first crab of *Allopetrolisthes angulosus* (Decapoda: Anomura: Porcellanidae) from Chile, reared in the laboratory. Journal of Crustacean Biology, 16: 730-747.
- Zar, J. H. 1999. Biostatistical Analysis. Prentice Hall, New Jersey, 4th edition, 663p. + 276 App.

Received: 15th Jan 2001

Accepted: 25th May 2001